An Urban Migraine: The Influence of Artificial Light at Night on Aquatic Primary Productivity

Benjamin Rubinoff
The Ohio State University, School of Environment and Natural Resources

Advisor: Dr. Mažeika Sullivan
Committee Members: Dr. Suzanne Gray, Dr. Lauren Pintor

Abstract: Artificial light at night (ALAN), or unnatural lighting produced by anthropogenic sources, has drastically altered the nighttime environment and is anticipated to increase as urban populations grow and electricity expands into previously unlit areas. The prevalence and predicted increases in ALAN have prompted a growing concern over light as an environmental pollutant (i.e., ecological light pollution), yet the effects of this stressor on ecosystem function remain largely unresolved. Here, the response of a common stream diatom (*Navicula pelliculosa*) to typical urban nighttime light levels was assessed through a 67-day laboratory experiment as measured using ash-free dry mass, gross primary productivity, and net primary productivity. Overall, diatom growth and productivity were significantly different over time and across light treatments. ALAN was associated with a decrease in ash-free dry mass and an increase in gross primary productivity, but was not related to net primary productivity. These patterns suggest that some species of diatoms may experience a physiological shift under ALAN. Since alterations in primary productivity can have strong bottom-up effects in aquatic systems, these results indicate that ALAN may have cascading trophic consequences.

Introduction

The relatively recent invention of artificial light at night (ALAN) has drastically altered the nighttime environment (reviewed in Longcore & Rich, 2004; Hölker et al., 2010). Artificial light at night, or unnatural lighting produced by anthropogenic sources, has become so extensive that two-thirds of the world population lives in areas where the night sky exhibits light levels much higher than natural levels (Cinzano et al., 2001; Horvath et al., 2009; Kyba & Hölker, 2013). Globally, ALAN is increasing, both through an increasing urban footprint as well as expansion of electricity into previously unlit environments. The prevalence and predicted

increases in ALAN have prompted a growing concern over night lighting as an environmental pollutant (i.e., ecological light pollution, ELP; reviewed in Longcore & Rich, 2004).

The substantial increase in the extent and intensity of artificial lighting over the past century has raised concern over potential impacts on biological and ecological processes – the consequences of which are not well understood (reviewed in Longcore & Rich, 2004). Even the term "light pollution" causes confusion. The term "light pollution" is commonly associated with astronomical light pollution, which occurs when artificial lights obscure the view of the night sky and its celestial bodies. Astronomical light pollution addresses the upcasting of light yet fails to address the downcasting of light, which alters natural light regimes in aquatic and terrestrial ecosystems (reviewed in Longcore & Rich, 2004). With artificial lighting increasing at around 3-6% globally each year, ALAN continues to alter even remote environments (Cinzano et al., 2001). Skyglow and direct sources of artificial lights have resulted in "perennial moonlight", with physiological, ecological, and evolutionary implications (Cinzano et al., 2001; Hölker et al., 2010; Kyba & Hölker, 2013).

Whereas knowledge on the effects of ALAN is incomplete, some adverse effects have been found and are predicted to influence both aquatic and terrestrial organisms. Among the impacts of ALAN, three primary categories of effects have been suggested: effects on behavioral and population ecology, effects on species interactions, and effects on ecosystem functions, the latter of which is arguably the least well understood (reviewed in Longcore and Rich 2004).

At the individual level, dispersal, recruitment, reproduction, and foraging behaviors of various taxa can be altered via nighttime lighting, influencing predator-prey interactions (Fraser & Metcalfe, 1997; Munday et al., 1998; Brüning et al., 2011; Perkin et al., 2011; Davies et al., 2012; Becker et al., 2013). For example, Salmonidae, an economically important family of fishes,

increase foraging efficiency with increased nighttime lighting intensities (Fraser & Metacalfe, 1997). Increased foraging in juvenile salmonids raises susceptibility to nighttime predation, potentially decreasing recruitment into fishable populations. Light pollution has the potential to influence fisheries by altering target populations, and therefore, affects both humans and entire ecosystems (Fraser & Metcalfe, 1997; Longcore & Rich, 2004; Perkin et al., 2011). Thus, any changes in individual animal behavior likely have implications for populations.

A brighter nightscape can extend diurnal activity across various animal taxa, affecting trophic interactions and structure through additional foraging opportunities (Longcore & Rich, 2004; Perkin et al., 2011; Becker et al., 2013). Multiple studies, across freshwater, terrestrial, and marine ecosystems, have found an increase in the relative abundance of predators and scavengers in brightly-lit communities (Longcore & Rich, 2004; Davies et al., 2012; Becker et al., 2013). These increased predator populations shift not only prey abundances, but whole community structure in habitat patches experiencing ALAN (Rydell, 1992). Predatory top-down control of large-bodied prey can cause trophic cascades, simultaneously affecting entire aquatic or terrestrial food webs by altering predation pressure and competition (Rydell, 1992; Davies et al., 2012; Becker et al., 2013). However, the physiological and trophic mechanisms by which species interactions are affected by ALAN remain largely unknown (Navara & Nelson, 2007).

Even when individual effects on species are small, the effects of ALAN can propagate through food webs to alter overall ecosystem function (Longcore & Rich, 2004). ALAN-induced trophic cascades may inhibit ecosystem services such as carbon storage and water filtration in both terrestrial and aquatic environments by altering trophic structure and the species that perform critical ecosystem functions (Davies et al., 2012; Becker et al., 2013). Additionally, effects of ALAN can propagate between ecosystems via resource subsidies. For example, the

magnitude and composition of aquatic-terrestrial fluxes of arthropods have been documented to change under artificial lighting (Meyer & Sullivan, 2013).

As reviewed above, many ecological effects of artificial lighting have been documented, indicating that ALAN is one of many environmental disturbances affecting aquatic and terrestrial ecosystems. Nonetheless, the novelty of this phenomenon warrants further research. Primary productivity, though crucial to ecosystem functioning, has not been studied extensively in the context of ALAN. Some terrestrial studies have found that artificial lighting can have phenological effects on leaf growth and senescence while others have found no effects on riparian vegetation (Cathey & Campbell, 1975; Davies et al., 2012). In freshwater systems, light pollution has the potential to alter in-stream productivity and phytoplankton abundances through both direct, physiological effects (Raven & Cockell, 2006; Poulin et al., 2014) and indirect, grazer effects (Moore et al., 2000; Perkin et al., 2011; Meyer & Sullivan, 2013). Physiologically, additional lighting may cause photoinhibition, the decrease in photosynthetic activity due to light stress (Richardson et al., 1983; Long et al., 1994; Lavaud et al., 2007). Phytoplankton are limited by light and nutrients, and in a steady-state laboratory setting, will produce biomass until being limited, then remain steady with nutrient uptake and productivity rates staying constant independent of biomass (Morel, 1987). However, any changes in light (e.g., as caused by ALAN) could result in changes in productivity due to physiological light limitations. ALAN has also recently been found to alter microbial productivity in soils by increasing photoautotroph (diatom) abundance and productivity and altering carbon processing (Hölker et al., 2015). Since both stream primary productivity and disturbance have been found to drive aquatic food webs and community structure (Death & Zimmerman, 2005), effects of ALAN on diatom productivity may offer insight into ecosystem-level processes.

Within this context, I investigated the effects of ALAN on diatom productivity. Overall, I predicted that algal biomass would reach a maximum as the experiment progressed with productivity remaining relatively constant. I anticipated that algal growth and productivity would be significantly different among elevated night lighting treatments. Specifically, I predicted that increasing ALAN intensities would elicit one of two responses: First, that increasing light intensities would increase diatom growth and productivity due to extended light availability. Or, that increasing light intensities would trigger a physiological constraint due to photoinhibition. These hypotheses were tested through a laboratory manipulation replicating ALAN levels commonly found in Columbus, Ohio streams.

Methods

The effects of ALAN on aquatic primary productivity were assessed via a 67-day laboratory experiment in spring 2015, using facilities of the Wilma H. Shiermeier Olentangy River Wetland Research Park. Three different light treatments were applied with four replicates each using twelve 18.9-L aquaria: control (0 lux), low (2-4 lux), and high (8-12 lux). The lighting treatments represented lux levels common in streams of urban Columbus, Ohio (see Meyer & Sullivan, 2013). Each aquarium received 12 h of daylight from a 65W grow bulb (~13,000 lux, similar to natural daytime illuminance values in small, shaded temperate streams; Finlay et al., 2011). Each of the three treatments was placed on different levels of a metal shelving unit (Fig. 1), separated by black plastic to prevent light contamination across treatments. Light treatments were produced using a strip of light emitting diodes (LEDs). The high treatment was subject to the full intensity of the LEDs while the intermediate treatment was screened to dampen the lighting intensity in order to match the intermediate light value. Treatment levels

were verified biweekly at the water surface with a ILT1700 Research Radiometer/Photometer (International Light Technologies; resolution: ±0.5% of the reading; Peabody, Massachusetts, USA).

Absolute irradiance was measured using a 600-µm UV/VIS fiber optic cable and a CC-3-UV-S cosine corrector attached to a JAZ EL200 spectrometer (OceanOptics, Inc., Jaz Spectrometer). The system was calibrated with a DH2000-CAL deuterium-halogen lamp. Downcasting irradiance just above the water surface measured for all tanks under "daytime" lighting conditions and "nighttime" treatment conditions (control, low, high). "Daytime" light was spectrally consistent across treatments, though with decreasing intensity from the top shelf of the rack to the bottom shelf. During "nighttime" recordings, the control treatment had no measureable light. The spectra measured under low and high treatments had similar spectral composition across wavelengths (see Supporting Information, Fig. S1, S2).

The bottom of each aquarium was lined with a single layer of 25.81-cm^2 unglazed ceramic tiles (a total of 32 tiles per tank). Based on algal community surveys in local streams, a commonly abundant diatom (*Navicula pelliculosa*; procured from UTEX, Austin, Texas) was introduced into each aquarium in equal concentrations (0.8 mL of concentrated culture per aquarium). Starting 18 days after introduction, the monoculture was assessed for ash-free dry mass (AFDM), gross primary productivity (GPP), and net primary productivity (NPP) twice per week over a period of 46 days, using a different tile per sampling event following the methods of Steinman & Lamberti (1996) and Power & Cardinale (2009). Individual tiles were removed from each tank and placed into individual Ziploc® (~950 mL) bags following Johnson et al. (2011). Using a HACH sensION™ MM156, dissolved oxygen (DO) was measured per incubation unit initially, 2 hours after a dark incubation, and 2 hours after a light incubation to estimate GPP.

The first two sampling dates used 1-h incubations and 500-mL Nalgene bottles as incubation containers; however, leaks and insufficient timing elicited a change in methods (note that the data from these two dates were not included in analysis). Respiration (R) was measured using the following equation:

$$\frac{DO_2 - DO_1}{A \times t} \times V_f \quad (1)$$

Where DO_2 is the dissolved oxygen (mg L^{-1}) after the dark incubation, DO_1 is the initial dissolved oxygen (mg L^{-1}), A is the tile area (m^2), t is the time (h), and V_f is the amount of water in the incubation unit (L). Net primary productivity (NPP) was measured using the following formula:

$$\frac{DO_3 - DO_2}{A \times t} \times V_f \quad (2)$$

Where DO_3 is the dissolved oxygen (mg L^{-1}) after the final light incubation. R and NPP were then summed to find gross primary productivity (GPP). Following GPP measurements, diatoms were scraped from tiles in the Ziplocs® and the contents of each unit were filtered through Whatman GF/F (47 mm, 0.7-µm pore size) filter papers. Filters were frozen and stored in the dark until AFDM analysis was conducted. Filters were then dried at 100˚C for 2 hours, weighed, combusted at 500˚C for one hour, and reweighed. Water levels within each aquarium were kept within a 6-cm range, filling tanks when needed with reverse osmosis deionized municipal water (AQUA FX5 Stage Mako RO/DI with chloramine removal filter; Pentair Aquatic Eco-Systems, Inc., Apopka, Florida).

Ash-free dry mass and NPP were cube-root transformed to meet assumptions of normality and homoscedasticity. Outliers that were multiple orders of magnitude different from the mean were removed due to sampling error. All statistical analyses were performed and graphs generated using JMP® v.11 (SAS Institute, Cary, North Carolina). Linear mixed models

(replicates nested within treatment) with time and the interaction of site*time as fixed factors were used to identify potential differences in primary productivity (AFDM, GPP, NPP) by lighting treatment (i.e., control, low, and high) over time. Post-hoc mean comparisons were performed using Tukey's HSD (Tukey, 1953).

Results

Conductivity, pH, and DO were variable across treatments with no observable trends (see Supporting Information; Table S1), giving me confidence that potential differences in water chemistry were not driving the observed responses in productivity. Water temperature was not different between treatments; however, it was significantly different over time with a sharp decrease on day 39 and a gradual increase back to similar temperatures at the beginning of sampling by day 67 (Fig. 2, $p < 0.0001$).

Overall, diatom productivity measurements varied considerably across treatments and time. Across all treatments, AFDM values ranged from 0.197 to 2.313 g cm^{-2} ($\bar{x}$ = 1.05 g cm^{-2}), GPP ranged from -123.9 to 191.1 mg m^{-2} h^{-1} ($\bar{x}$ = 38.37 mg m^{-2} h^{-1}), and NPP ranged from -48.9 to 175.6 mg m^{-2} h^{-1} ($\bar{x}$ = 25.13 mg m^{-2} h^{-1}) (see Supporting Information; Table S2). Tank productivity was significantly different among treatments; however, productivity did not differ significantly within treatments (see Supporting Information; Fig. S3).

Linear mixed models indicated that all measures of productivity were significantly different over time. Ash-free dry mass significantly increased over time across all treatments (Fig. 3a, $p < 0.0001$). Gross primary productivity was variable; however, time emerged as a significant factor (Fig. 3b, $p < 0.0001$). Net primary productivity was variable as well with a decrease in values from day 25 to day 46, increasing from day 46 to day 63, then returning to values similar

at the start of the experiment on day 67 (Fig. 3c, $p < 0.0001$). Trends in productivity were similar across treatments with minor variations, suggesting consistent differences in average productivity among treatments over time (Fig. 4).

Although time exerted the greatest effect on primary productivity measures, treatment also emerged as a significant factor. Based on time-averaged values, AFDM decreased with increasing light intensities (Fig. 5a, $p = 0.032$). The no-light, control treatment exhibited the highest AFDM ($\bar{x}$ = 1.067 g cm^{-2} ± 3.361E-2), the low treatment had an intermediate value ($\bar{x}$ = 1.001 g cm^{-2} ± 3.406E-2), and the high treatment resulted in the lowest value ($\bar{x}$ = 0.915 g cm^{-2} ± 3.370E-2). Gross primary productivity in the control treatment ($\bar{x}$ = 30.212 mg m^{-2} h^{-1} ± 3.406) was significantly lower than in the low ($\bar{x}$ = 43.902 mg m^{-2} h^{-1} ± 3.406) or high ($\bar{x}$ = 42.108 mg m^{-2} h^{-1} ± 3.371) treatments, and thus gross primary productivity followed the opposite trend: ALAN resulted in increased GPP (Fig. 5b, $p = 0.038$). Net primary productivity was not different by treatment (Fig 5c, $p = 0.515$). There was no interaction effect of time and treatment on AFDM ($p = 0.060$) or NPP ($p = 0.301$), yet there was a significant interaction effect on GPP ($F_{22,120} = 1.90$, $p = 0.018$).

Discussion

Artificial light at night has the potential to be a significant disturbance in aquatic ecosystems (Longcore & Rich, 2004; Perkin et al., 2011; Davies et al., 2012). Among other ecological consequences across various scales, ALAN can strongly alter trophic dynamics (Rydell, 1992; Davies et al., 2012; Becker et al., 2013). In this study, I found complex effects of ALAN on diatom productivity. Although diatom biomass generally increased and productivity remained fairly constant following water temperature patterns over time across all lighting levels,

the response to ALAN was different across treatments. The highest light levels of the study (8-12 lux) prompted a decrease in AFDM, whereas even the lowest values (2-4 lux) elicited an increase in GPP. This suggests that even low ALAN levels may elicit threshold responses in primary productivity and biomass. Therefore, large magnitude effects (as seen in GPP) from small ALAN values might be expected to cause cascades through bottom-up processes. Overall, these results have implications for predator-prey dynamics and ecosystem processes in aquatic systems through both direct and indirect mechanisms.

AFDM slowly increased over the course of the experiment, leveling off after day 23 (Fig. 3a; Fig. 4a), supporting my first hypothesis. This pattern likely reflects the continued growth and establishment of the population until resource limitations or stress stabilized diatom growth (Grimm & Fisher, 1989). Gross primary productivity and NPP tended to decrease from day 25 to day 46, increasing back toward values produced at the beginning of the experiment on day 67 (Fig. 3b,c; Fig. 4b,c). This trend, also seen in water temperature (Fig. 2), affirms the positive relationship of water temperature and productivity rates, a pattern documented in stream diatom productivity (Morin et al., 1999). Changes in GPP and NPP were consistent with water temperature; however, at constant temperatures, productivity would have probably remained fairly constant, supporting my hypothesis. I believe that if I had run the experiment longer, AFDM, GPP, and NPP would have remained fairly constant over time following steady-state patterns documented in other laboratory diatom cultivations (Morel, 1987). A useful next step in this research could be examining the effects of ALAN on diatom species at different temperature and nutrient levels, lending insight into how different diatom species might react to the global influence of ALAN across their geographical ranges.

Each of the predicted outcomes was expressed in different productivity measurements. Overall, ALAN led to significantly higher GPP and lower AFDM. Decreases in biomass seen in AFDM with increased ALAN may indicate that growth is inhibited under the additional stress generated by extended lighting regimes (Fig. 5a). Photoinhibition resulting from light stress, as is seen in decreased diatom biomass production, has been documented in phytoplankton, potentially suggesting that this result has implications across diatom species (Richardson et al., 1983; Long et al., 1994). However, photoinhibition was not seen in GPP; increased ALAN resulted in greater productivity (Fig. 5b). These results suggest that *N. pelliculosa* may have greater photoprotection, and potential energetic benefits from extended lighting. Studies on various diatom species validate the higher photoprotective capacity of this freshwater species (Richardson et al., 1983; Lavaud et al., 2007).

Although GPP was significantly higher in the low ALAN treatment, the use of AFDM as a growth measurement is limited. Ash-free dry mass is a measurement of organic carbon, live or dead, and therefore does not typically quantify living biomass only. If there were a significant proportion of the biomass represented by dead cells, ALAN might not necessarily lead to more biomass across longer periods of time, supporting the results seen in GPP. Alternative methods of measuring productivity (e.g., chlorophyll a) could benefit future studies in this regard.

Some species of diatoms and cyanobacteria have light compensation points of growth and photosynthesis at low light levels (Hölker et al., 2015). One possible mechanism for this is that the low ALAN values applied in this experiment caused state transitions, or short-term acclimations allowing the diatoms to more efficiently balance energy distribution between the two photosynthesis systems (Hölker et al., 2015). This could explain why productivity (GPP) was significantly high even at low lighting levels. While most studies on photoinhibition have

been conducted in the context of seasonal or system-dependent properties (i.e. open ocean or shallow coastal estuary), the results of this experiment and previous studies suggest shifts in primary-producer species assemblage. For example, some marine photolithotrophic algae can grow under ~0.05 lux (slightly above the light of a full moon on a clear night; Raven & Cockell, 2006).

Artificial and natural lighting act in tandem with other environmental variables to regulate community structure through bottom-up processes and other indirect effects (Longcore & Rich, 2004; Perkin et al., 2011). Changes in lighting regimes can induce fitness-based shifts in algal community composition, increasing harmful algal blooms (Richardson et al., 1983; Moore et al., 2000; Perkin et al., 2011) and promoting species with varying productivity and nutrient processing rates. Therefore, increasing ALAN could result in global changes in not only the prevalence of harmful algal blooms (HAB), but also overall ecosystem functions through direct (physiological) and indirect (trophic cascade) effects.

This project quantified the direct effects of ALAN on one diatom species. However, further research should focus on productivity responses of different algal species (including those responsible for HABs). Additionally, to better understand the mechanisms of ALAN's effects, indirect effects (such as trophic interactions) should be quantified across taxa in tandem with varying environmental variables to gain a better understanding of effects in complex natural systems. This research project contributes to ongoing efforts in Dr. Mažeika Sullivan's laboratory group to understand and quantify the consequences of artificial lighting at night on aquatic-riparian ecosystem structure and function. In particular, findings from this research will elucidate potential mechanisms driving documented changes in food-web architecture and

ecosystem function (e.g., energy flows between aquatic and terrestrial systems). Thus, this work represents both a stand-alone project as well as an integral part of a broader research effort.

Acknowledgements

I am grateful to have received the Honors Enrichment Grant from The Ohio State University. This research was also funded by an honors scholarship from the School of Environment and Natural Resources. I am very grateful to have received help and support from Lars Meyer, Katie Hossler, and Brent Macolley.

References

Becker, A., Whitfield, A. K., Cowley, P. D., Naesje, T. F., & Jarnegren, J. (2013). Potential effects of artificial light associated with anthropogenic infrastructure on the abundance and foraging behaviour of estuary-associated fishes. *Journal of Applied Ecology, 50,* 1, 43-50.

Brüning, A., Hölker, F., & Wolter, C. (2011). Artificial light at night: implications for early life stages development in four temperate freshwater fish species. *Aquatic Sciences, 73,* 1, 143-152.

Cathey, H. M., & Campbell, L. E. (1975). Security lighting and its impact on the landscape. *Journal of Arboriculture, 1*(10), 181.

Cinzano, P., Falchi, F., & Elvidge, C. D. (2001). The first World Atlas of the artificial night sky brightness. *Monthly Notices of the Royal Astronomical Society, 328,* 3, 689-707.

Davies, T. W., Bennie, J., & Gaston, K. J. (2012). Street lighting changes the composition of invertebrate communities. *Biology Letters, 8,* 5, 764-7.

Death, R. G., & Zimmerman, E. M. (2005). Interaction between disturbance and primary productivity in determining stream invertebrate diversity. *Oikos, 111,* 2, 392-402.

Finlay, J. C., Hood, J. M., Limm, M. P., Power, M. E., Schade, J. D., & Welter, J. R. (2011). Light-mediated thresholds in stream-water nutrient composition in a river network. *Ecology, 92,* 1, 140-50.

Fraser, N. H. C., & Metcalfe, N. B. (1997). The costs of becoming nocturnal: feeding efficiency in relation to light intensity in juvenile Atlantic Salmon. *Functional Ecology, 11,* 3, 385.

Grimm, N. B., & Fisher, S. G. (1989). Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *Journal of the North American Benthological Society, 8,* 4, 293-307.

Hölker, F., Moss, T., Griefahn, B., Kloas, W., Voigt, C. C., Henckel, D., Hänel, A., Kappeler, P., Völker, S., Schwope, A., Franke, S., Uhrlandt, D., Fischer, J., Klenke, R., Wolter, C., Tockner, K. (2010). The dark side of light: A transdisciplinary research agenda for light pollution policy. *Ecology & Society, 15,* 4.

Hölker, F., Wurzbacher, C., Weissenborn, C., Monaghan, M. T., Holzhauer, S. I. J., & Premke, K. (2015). Microbial diversity and community respiration in freshwater sediments influenced by artificial light at night. *Philosophical Transactions of the Royal Society B: Biological Sciences, 370,* 1667, 20140130.

Horvath, G., Kriska, G., Malik, P., & Robertson, B. (2009). Polarized light pollution: a new kind of ecological photopollution. *Frontiers in Ecology and the Environment, 7,* 6, 317-325.

Johnson, K. A., Steinman, A. D., Keiper, W. D., & Ruetz, C. R. (2011). Biotic responses to low-concentration urban road runoff. *Journal of the North American Benthological Society, 30,* 3, 710-727.

Kyba, C. C. M., & Hölker, F. (2013). Do artificially illuminated skies affect biodiversity in nocturnal landscapes?. *Landscape Ecology, 28,* 9, 1637-1640.

Lavaud, J., Strzepek, R. F., & Kroth, P. G. (2007). Photoprotection capacity differs among diatoms: Possible consequences on the spatial distribution of diatoms related to fluctuations in the underwater light climate. *Limnology and Oceanography, 52,*3, 1188-1194.

Long, S. P., Humphries, S., & Falkowski, P. G. (1994). Photoinhibition of Photosynthesis in Nature. *Annual Review of Plant Physiology and Plant Molecular Biology, 45,* 633-662.
Longcore, T., & Rich, C. (2004). Ecological light pollution. *Frontiers in Ecology and the Environment, 2,* 4, 191-198.
Meyer, L. A., & Sullivan, M. P. (2013). Bright lights, big city: Influences of ecological light pollution on reciprocal stream–riparian invertebrate fluxes. *Ecological Applications, 23*(6), 1322-1330.
Moore, M. V., Pierce, S. M., Walsh, H. M., Kvalvik, S. K., & Lim, J. D. (2000). Urban light pollution alters the diel vertical migration of Daphnia. *Proceedings- International Association of Theoretical and Applied Limnology, 27,* 779-782.
Morel, F. M. M. (1987). Kinetics of nutrient uptake and growth in phytoplankton. *Journal of Phycology, 23,* 2, 137-150.
Morin, A., Lamoureux, W., & Busnarda, J. (1999). Empirical models predicting primary productivity from chlorophyll a and water temperature for stream periphyton and lake and ocean phytoplankton. *Journal of the North American Benthological Society, 18,* 3, 299-307.
Munday, P. L., Jones, G. P., Oehman, M. C., & Kaly, U. L. (1998). Enhancement of recruitment to coral reefs using light attractors. *Bulletin of Marine Science Miami, 63,* 3, 581-588.
Navara, K. J., & Nelson, R. J. (2007). The dark side of light at night: physiological, epidemiological, and ecological consequences. *Journal of Pineal Research, 43,* 3, 215-224.
Perkin, E. K., Hölker, F., Richardson, J. S., Sadler, J. P., Wolter, C., & Tockner, K. (2011). The influence of artificial light on stream and riparian ecosystems: questions, challenges, and perspectives. *Ecosphere, 2,* 11.
Poulin, C., F. Bruyant, M.-H. Laprise, A. M. Cockshutt, J. M.-R. Vandenhecke, Y. Huot. (2014). The impact of light pollution on diel changes in the photophysiology of Microcystis aeruginosa. *Journal of Plankton Research*, 36, 286-291.
Power, L. D., & Cardinale, B. J. (2009). Species richness enhances both algal biomass and rates of oxygen production in aquatic microcosms. *Oikos, 118,* 11, 1703-1711.
Raven, J. A., & C. S. Cockell. (2006). Influence on photosynthesis of starlight, moonlight, planetlight, and light pollution (reflections on photosynthetically active radiation in the universe). *Astrobiology*, 6, 668-675.
Richardson, K., Beardall, J., & Raven, J. A. (1983). Adaptation of unicellular algae to irradiance: an analysis of strategies. *New Phytologist, 93,* 2, 157-191.
Rydell, J. (1992). Exploitation of insects around streetlamps by bats in Sweden. *Functional Ecology, 6,* 6, 744.
Steinman, A.D. & Lamberti, G.A. (1996). Biomass and pigments of benthic algae. P. 297. In "Methods in Stream Ecology". Hauer, F.R. & Lamberti, G.A. (eds). Academic Press, San Diego, CA.
Tukey, J.W. (1953). The problem of multiple comparisons. Unpublished report. Princeton University.

Figures

Figure 1. Laboratory set up for lighting experiment. Each shelf constitutes the control (top), low (middle), and high (bottom) treatments. Each 18.927 L tank received 12 h of daylight from a 65W grow bulb. ALAN levels were applied at night to the control (12 h of ~0 lux), low (12 h of ~3-5 lux), and high (12 h of ~15 lux) treatments. Each shelf was lined with opaque black plastic to prevent treatment light contamination.

Figure 2. Mean water temperature (°C) sampled weekly over the 42-day sampling period ($F_{6,77}$ = 14.549, $p < 0.0001$). Significant pairwise differences are indicated by letters A,B,C,D (Tukey's HSD, $p < 0.05$). Error bars represent $\pm$ 1 SE**.**

Figure 3. Diatom productivity over time averaged among control, low, and high treatments: (a) AFDM ($F_{11,128} = 5.25$, $p < 0.0001$), (b) gross primary productivity (GPP: $F_{11,131} = 29.64$, $p <$ 0.0001), and (c) NPP ($F_{11,131} = 18.13$, $p < 0.0001$). Statistical analyses use cube-root transformed data for AFDM and NPP; however, the figure presents raw data. Significant pairwise differences are indicated by letters A,B,C,D,E (Tukey's HSD, $p < 0.05$). Negative values indicate increased respiration and are a result of equations used and equipment sensitivity. Error bars represent $\pm$ 1 SE.

Figure 4. Diatom productivity over time for control (grey, 0 lux), low (green, 2-4 lux), and high (blue, 8-12 lux) treatments: (a) AFDM ($F_{11,128} = 5.25$, $p < 0.0001$), (b) GPP ($F_{11,131} = 29.64$, $p <$ 0.0001), and (c) NPP ($F_{11,131} = 18.13$, $p < 0.0001$). Statistical analyses use cube-root transformed data for AFDM and NPP; however, the figure presents raw data.

Figure 5. Diatom productivity averaged over the experiment among control (~0 lux), low (2-4 lx), and high (8-12 lux) treatments for (a) AFDM ($F_{2,137} = 5.10$, $p = 0.032$), (b) GPP ($F_{2,140} = 4.78$, $p = 0.038$), and (c) NPP ($F_{2,140} = 0.72$, $p = 0.515$). Statistical analyses use cube-root transformed data for AFDM and NPP; however, the figure presents raw data. Significant pairwise differences are indicated by letters A,B (Tukey's HSD, $p < 0.05$). Error bars represent $\pm$ 1 SE.

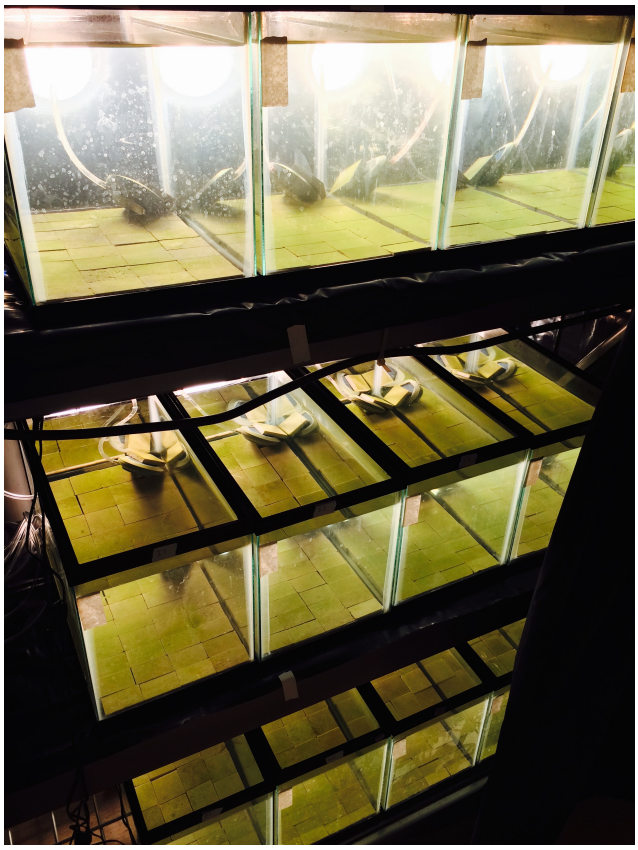

Figure 1

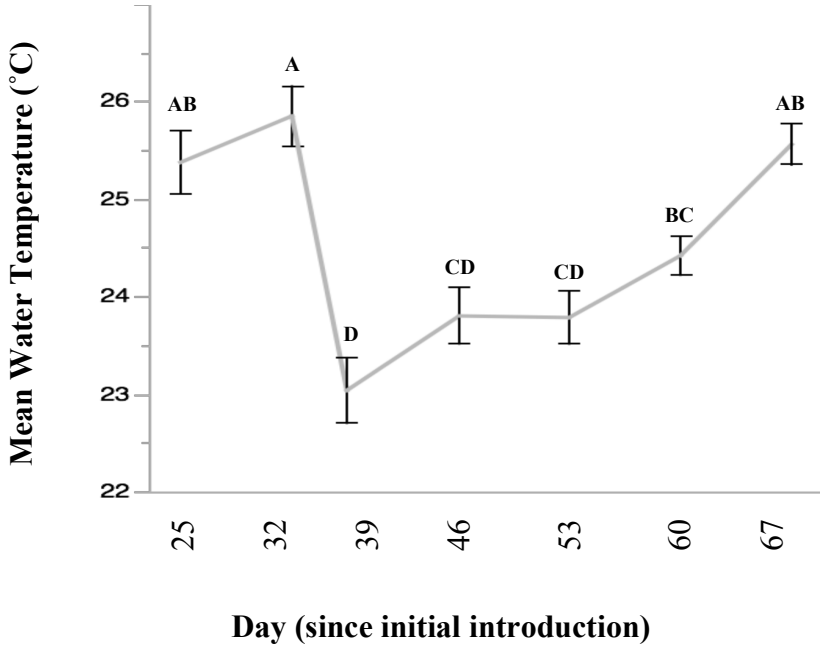
Mean Water Temperature (°C)
26
25
24
23
22
AB
A
D
CD
CD
BC
AB
25
32
39
46
53
60
67
Day (since initial introduction)

Figure 2

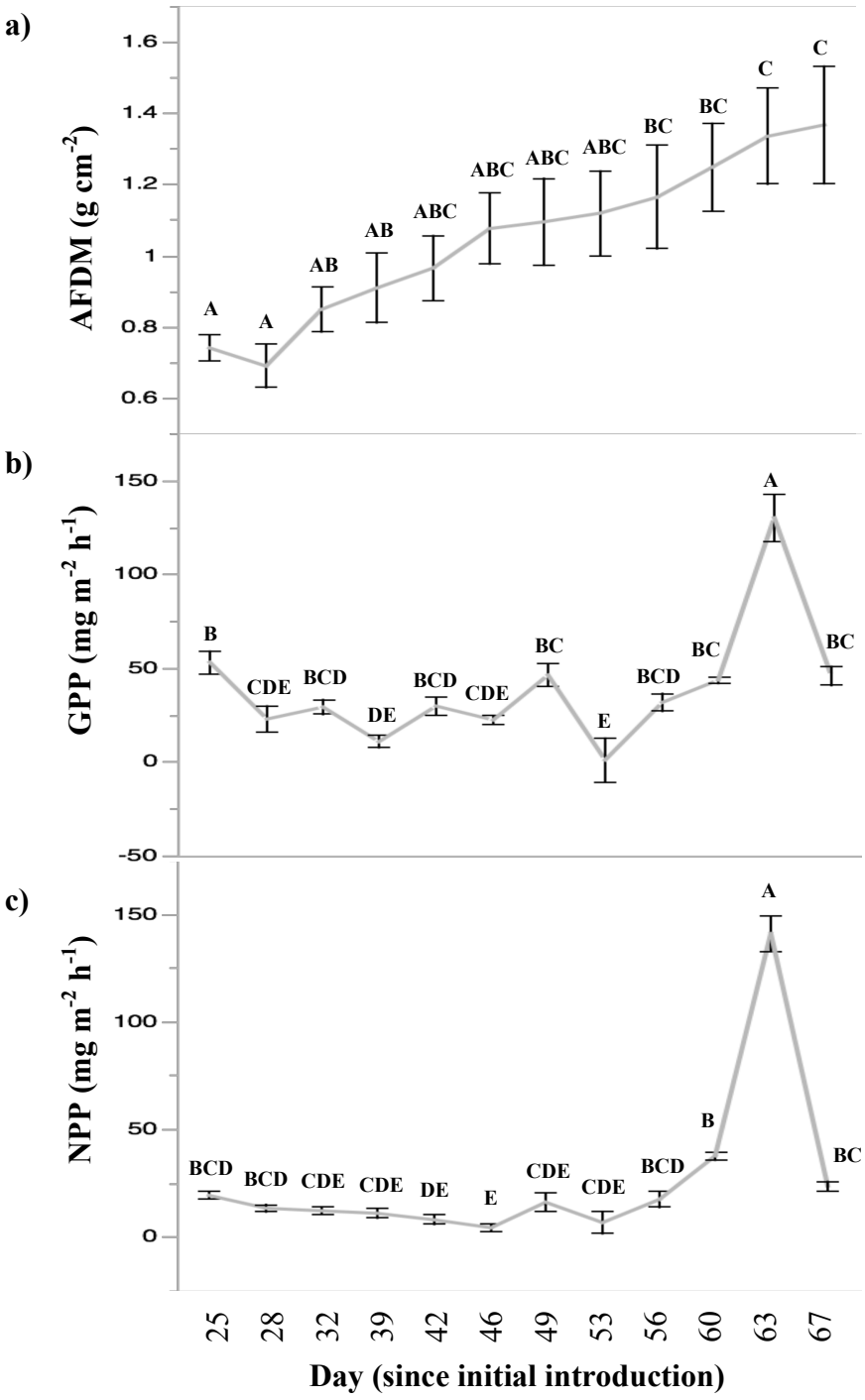
a)
AFDM (g cm-2)
1.6
1.4
1.2
1
0.8
0.6
A
A
AB
AB
ABC
ABC
ABC
ABC
BC
BC
C
C
b)
GPP (mg m-2 h-1)
150
100
50
0
-50
B
CDE
BCD
DE
BCD
CDE
BC
E
BCD
BC
A
BC
c)
NPP (mg m-2 h-1)
150
100
50
0
BCD
BCD
CDE
CDE
DE
E
CDE
CDE
BCD
B
A
BC
25
28
32
39
42
46
49
53
56
60
63
67
Day (since initial introduction)

Figure 3

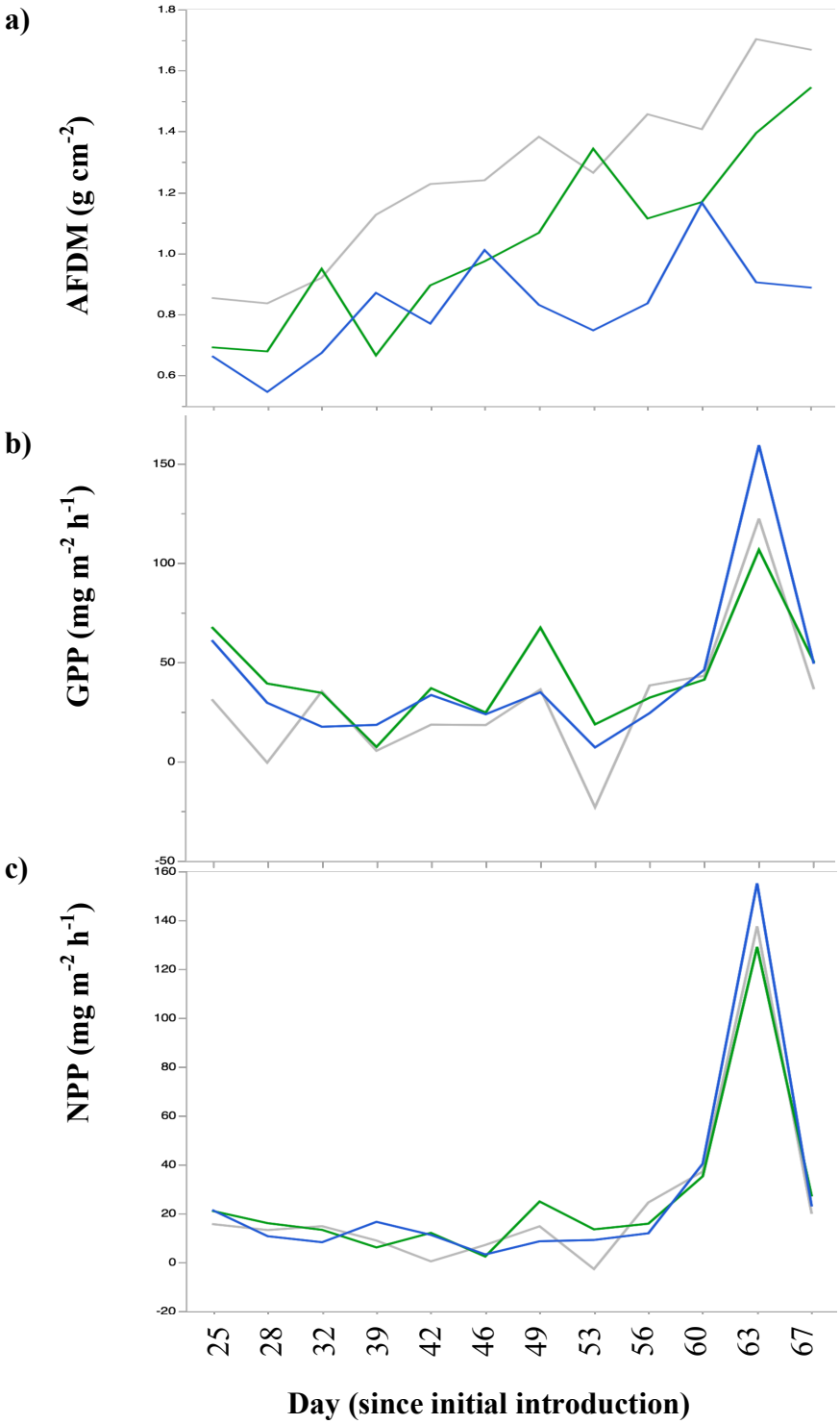
a)
AFDM (g cm-2)
1.8
1.6
1.4
1.2
1.0
0.8
0.6
b)
GPP (mg m-2 h-1)
150
100
50
0
-50
c)
NPP (mg m-2 h-1)
160
140
120
100
80
60
40
20
0
-20
25
28
32
39
42
46
49
53
56
60
63
67
Day (since initial introduction)

Figure 4

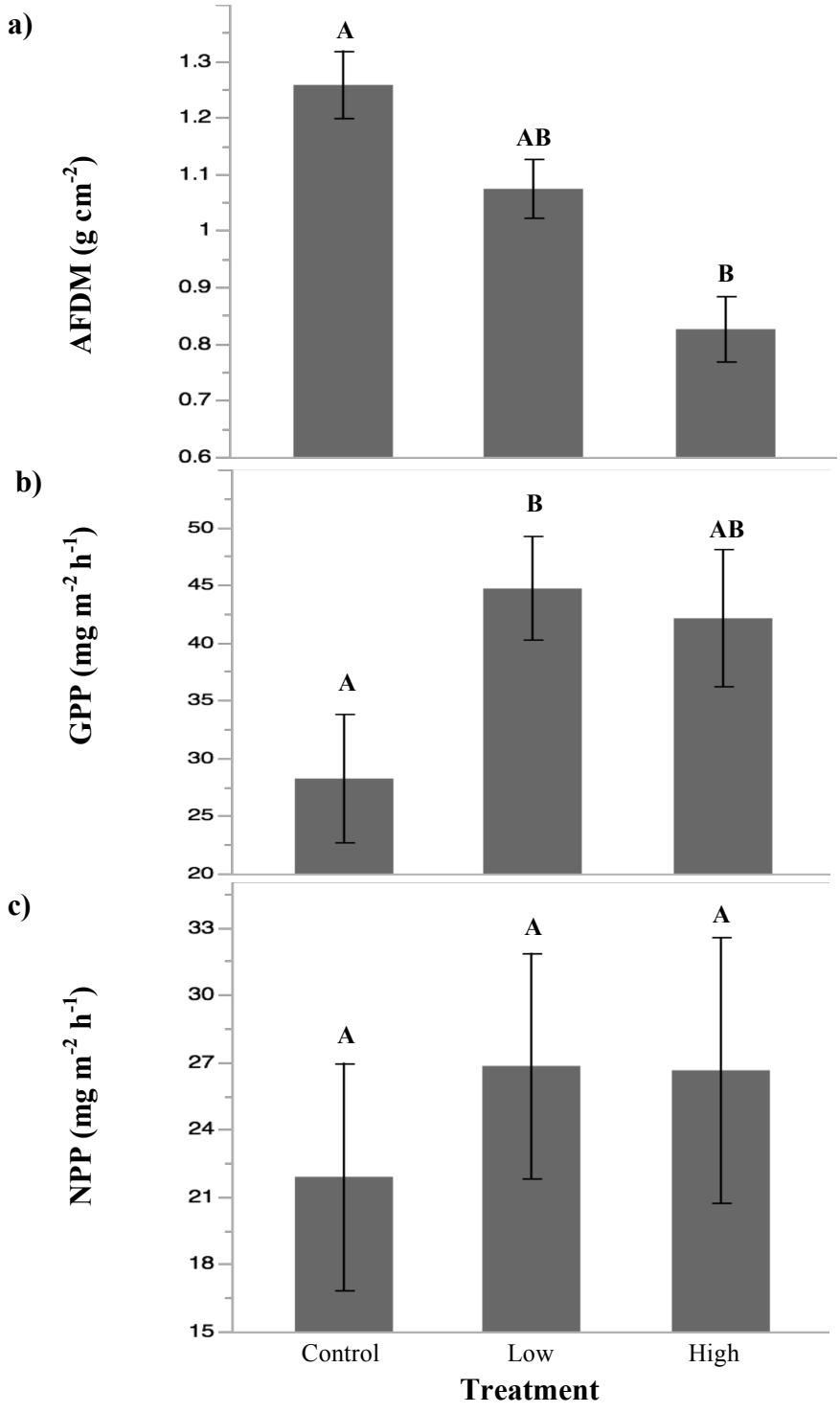
a)
AFDM (g cm-2)
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
A
AB
B
b)
GPP (mg m-2 h-1)
50
45
40
35
30
25
20
B
AB
A
c)
NPP (mg m-2 h-1)
33
30
27
24
21
18
15
A
A
A
Control
Low
High
Treatment

Figure 5

Supporting Information

Table S1. Water-chemistry data over the course of the 67-day experiment. Day 25 represents the first day of sampling, 25 days after the diatom introduction. Each tank is labeled by treatment (C = control, L = low, H = high) and replicate (1, 2, 3, 4).

Day	Time	Tank	pH	Conductivity (uS/cm)	DO (mg/L)	Temperature (ºC)
25	16:30	C1	8.7	282	9.25	24.2
25	16:30	C2	8.78	328	9.27	24.5
25	16:30	C3	8.8	282	9.24	24.3
25	16:30	C4	8.78	394	9.45	23.3
25	16:30	L1	8.8	326	9.16	25.5
25	16:30	L2	8.79	316	8.99	26.7
25	16:30	L3	8.77	416	8.87	26.9
25	16:30	L4	8.83	366	9.17	25.7
25	16:30	H1	8.82	308	9.1	25.3
25	16:30	H2	8.78	355	8.91	26.1
25	16:30	H3	8.79	322	8.99	26.3
25	16:30	H4	8.85	300	9.11	25.7
32	16:17	C1	8.7	281	9.16	24.7
32	16:17	C2	8.8	321	9.15	25
32	16:17	C3	8.8	283	9.04	24.8
32	16:17	C4	8.79	382	9.18	23.9
32	16:17	L1	8.77	316	8.81	26
32	16:17	L2	8.77	316	8.67	27.1
32	16:17	L3	8.74	404	8.53	27.4
32	16:17	L4	8.78	356	8.84	26.2
32	16:17	H1	8.8	302	8.69	25.8
32	16:17	H2	8.76	347	8.53	26.6
32	16:17	H3	8.82	315	8.67	26.7
32	16:17	H4	8.83	289	8.76	26
39	13:28	C1	8.96	345	10.03	21.9
39	13:28	C2	8.95	408	9.84	22
39	13:28	C3	8.97	357	9.89	21.8
39	13:28	C4	8.98	541	10.04	21.1
39	13:28	L1	8.95	370	9.65	23.5
39	13:28	L2	8.91	370	9.52	24.1
39	13:28	L3	8.89	479	9.39	24.3
39	13:28	L4	8.94	442	9.68	23.3
39	13:28	H1	8.93	352	9.52	23.6
39	13:28	H2	8.91	410	9.38	24
39	13:28	H3	8.98	370	9.53	24.2
39	13:28	H4	9	340	9.56	23.9
46	13:28	C1	8.97	328	9.76	22.7
46	13:28	C2	8.94	373	9.57	22.8
46	13:28	C3	8.93	329	9.59	22.7
46	13:28	C4	8.96	471	9.7	22

46	13:28	L1	8.92	352	9.41	23.9
46	13:28	L2	8.91	349	9.31	24.6
46	13:28	L3	8.87	442	9.18	24.8
46	13:28	L4	8.93	411	9.36	24
46	13:28	H1	8.92	333	9.3	24.1
46	13:28	H2	8.89	383	9.17	24.7
46	13:28	H3	8.94	352	9.26	24.9
46	13:28	H4	9	321	9.32	24.4
53	13:15	C1	8.83	291	10.07	22.7
53	13:15	C2	8.8	319	9.88	22.9
53	13:15	C3	8.83	272	9.86	22.7
53	13:15	C4	8.81	394	9.99	22.1
53	13:15	L1	8.82	319	9.76	23.8
53	13:15	L2	8.79	331	9.49	24.6
53	13:15	L3	8.77	401	9.46	24.7
53	13:15	L4	8.85	366	9.66	24
53	13:15	H1	8.83	312	9.51	24.2
53	13:15	H2	8.82	349	9.42	24.6
53	13:15	H3	8.86	319	9.49	24.8
53	13:15	H4	8.9	297	9.55	24.3
60	13:16	C1	8.92	292	9.27	23.6
60	13:16	C2	8.93	308	9.24	23.8
60	13:16	C3	8.94	264	9.14	23.6
60	13:16	C4	8.92	393	9.2	23.3
60	13:16	L1	8.94	316	9.16	24.4
60	13:16	L2	8.91	366	8.88	25.1
60	13:16	L3	8.94	390	8.87	24.8
60	13:16	L4	8.95	359	9.04	24.4
60	13:16	H1	8.93	313	8.89	24.7
60	13:16	H2	8.91	349	8.77	25.2
60	13:16	H3	8.94	319	8.84	25.3
60	13:16	H4	8.98	299	8.91	24.8
67	13:15	C1	8.92	294	9.96	24.6
67	13:15	C2	9.02	307	9.95	25
67	13:15	C3	9	274	9.8	24.8
67	13:15	C4	9.01	390	9.91	24.3
67	13:15	L1	9	312	9.78	25.6
67	13:15	L2	8.97	352	9.49	26.4
67	13:15	L3	8.99	383	9.48	26.1
67	13:15	L4	9.03	358	9.66	25.6
67	13:15	H1	9	305	9.54	25.8
67	13:15	H2	8.97	343	9.42	26.3
67	13:15	H3	9	313	9.46	26.4
67	13:15	H4	9.01	299	9.46	25.8

Table S2. Raw mean ± SE productivity for **(a)** ash-free dry mass (g cm^{-2}), **(b)** gross primary productivity (mg m^{-2} h^{-1}), and **(c)** net primary productivity (mg m^{-2} h^{-1}). Day 25 represents the first day of measurements.

a)

Day	Control (0 lux)	Low (2-4 lux)	High (8-12 lux)
25	0.854 ± 0.055	0.692 ± 0.043	0.662 ± 0.024
28	0.837 ± 0.093	0.679 ± 0.030	0.546 ± 0.069
32	0.920 ± 0.113	0.950 ± 0.080	0.674 ± 0.099
39	1.127 ± 0.130	0.666 ± 0.191	0.871 ± 0.146
42	1.228 ± 0.141	0.896 ± 0.076	0.770 ± 0.167
46	1.240 ± 0.071	0.974 ± 0.043	1.011 ± 0.297
49	1.383 ± 0.176	1.068 ± 0.126	0.832 ± 0.258
53	1.265 ± 0.231	1.344 ± 0.115	0.748 ± 0.134
56	1.457 ± 0.318	1.115 ± 0.065	0.837 ± 0.248
60	1.407 ± 0.191	1.169 ± 0.030	1.166 ± 0.343
63	1.703 ± 0.212	1.395 ± 0.107	0.906 ± 0.187
67	1.668 ± 0.176	1.543 ± 0.290	0.888 ± 0.261

b)

Day	Control (0 lux)	Low (2-4 lux)	High (8-12 lux)
25	30.925 ± 6.431	67.345 ± 8.797	60.685 ± 4.644
28	-0.573 ± 3.118	39.288 ± 12.532	29.595 ± 9.041
32	35.370 ± 7.430	34.580 ± 5.637	17.518 ± 4.532
39	5.420 ± 5.375	7.370 ± 4.574	18.460 ± 4.888
42	18.583 ± 8.205	36.930 ± 8.323	33.520 ± 5.602
46	18.373 ± 4.015	24.635 ± 1.816	23.825 ± 5.470
49	36.318 ± 7.156	67.450 ± 8.068	34.910 ± 6.664
53	-22.995 ± 33.835	18.728 ± 6.142	7.113 ± 2.779
56	38.335 ± 14.040	32.188 ± 3.480	24.413 ± 3.060
60	43.210 ± 3.674	41.263 ± 2.937	46.208 ± 3.435
63	122.303 ± 15.647	106.638 ± 25.166	159.293 ± 13.267
67	36.943 ± 1.422	50.460 ± 4.009	49.755 ± 15.217

c)

Day	Control (0 lux)	Low (2-4 lux)	High (8-12 lux)
25	15.610 ± 2.154	20.965 ± 2.192	21.218 ± 3.396
28	13.218 ± 2.042	16.028 ± 4.521	10.690 ± 1.979
32	14.795 ± 2.946	13.300 ± 1.903	8.223 ± 3.040
39	8.920 ± 3.775	6.107 ± 2.358	16.573 ± 3.306
42	0.408 ± 0.958	12.058 ± 3.834	11.238 ± 2.520
46	7.110 ± 3.749	2.380 ± 0.952	3.235 ± 2.994
49	14.750 ± 6.163	24.903 ± 8.296	8.613 ± 5.245
53	-2.738 ± 15.741	13.503 ± 1.249	9.150 ± 1.036
56	24.510 ± 10.931	15.815 ± 1.569	11.898 ± 2.258
60	37.155 ± 5.442	35.215 ± 1.932	40.365 ± 2.681
63	137.540 ± 16.715	129.113 ± 16.932	155.125 ± 7.822
67	20.270 ± 1.927	27.373 ± 1.971	23.288 ± 5.628

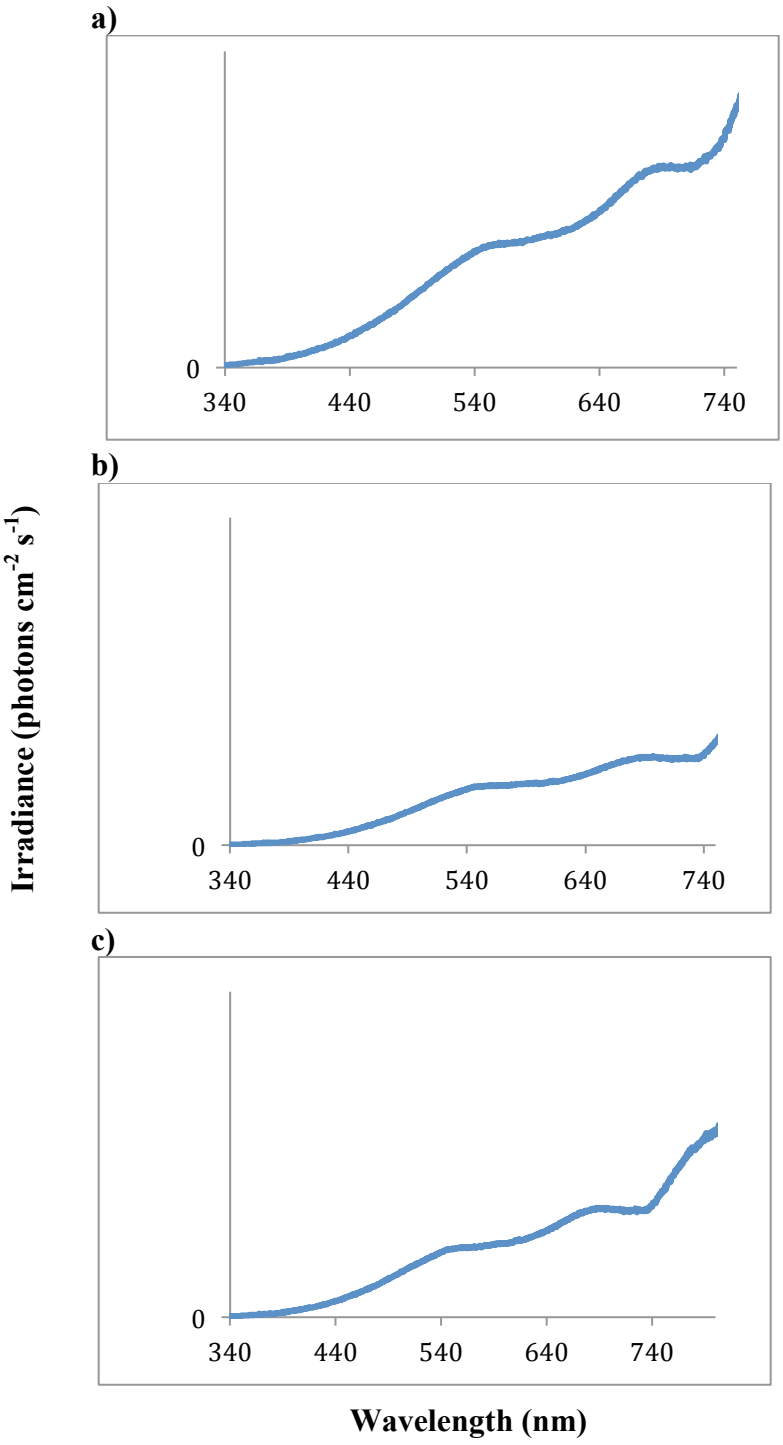

Figure S1. Daytime downwelling irradiance measured for (a) one control tank (0 lux), (b) one low tank (2-4 lux), and (c) one high tank (8-12 lux).

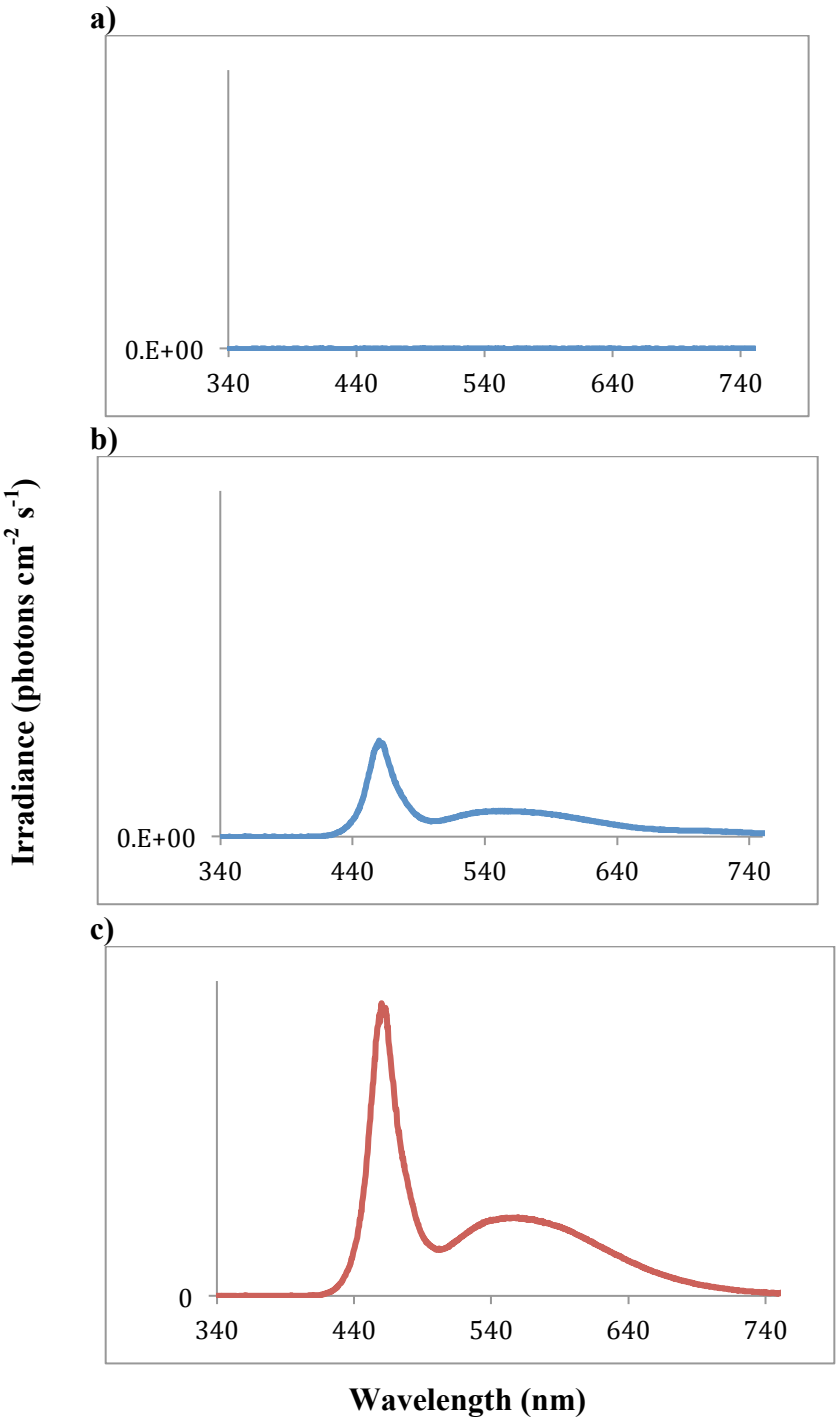

Figure S2. Nighttime downwelling irradiance measured for (a) one control tank (0 lux), (b) one low tank (2-4 lux), and (c) one high tank (8-12 lux).

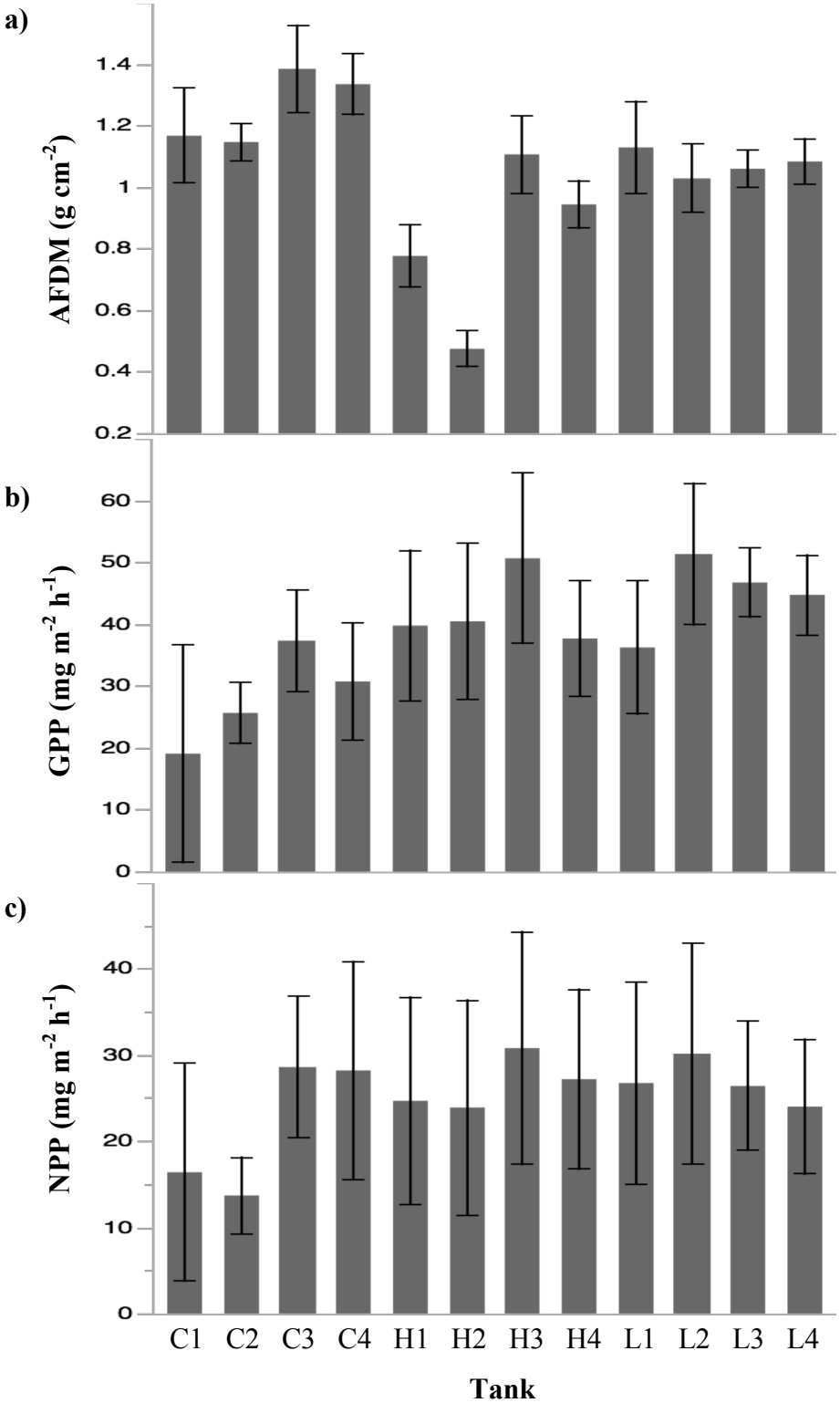

Figure S3. Diatom productivity across tanks for (a) AFDM, (b) gross primary productivity (GPP), and (c) NPP. Tanks are labeled by treatment (C = control, H = high, L = low) and replicate (1-4). Error bars represent ± 1 SE.